

On *Pieris (Artogeia) marginalis macdunnoughii* Remington (Pieridae). Part II.

S. R. Bowden

Lydeard, Merryfield Way, Storrington, W. Sussex, RH20 4NS, U.K.

Abstract. The crossing of *Pieris* ssp. *macdunnoughii* (almost without marking on the upperside) with a European *P. napi* produced F₁ male hybrids even more heavily marked than normal *napi*. It was not thought that the funebris gene which was present in the European stock was responsible. The female hybrids, carrying an approximation to the *napi* female pattern, showed slight asymmetry of marking, and "smudging". Comparable results from other wide crosses within the *napi* group suggest that these, unlike closer hybrids, often suffer disturbance of the canalizing mechanisms which control patterns. In the present case abnormally short diapause failed to produce the full "spring" characters.

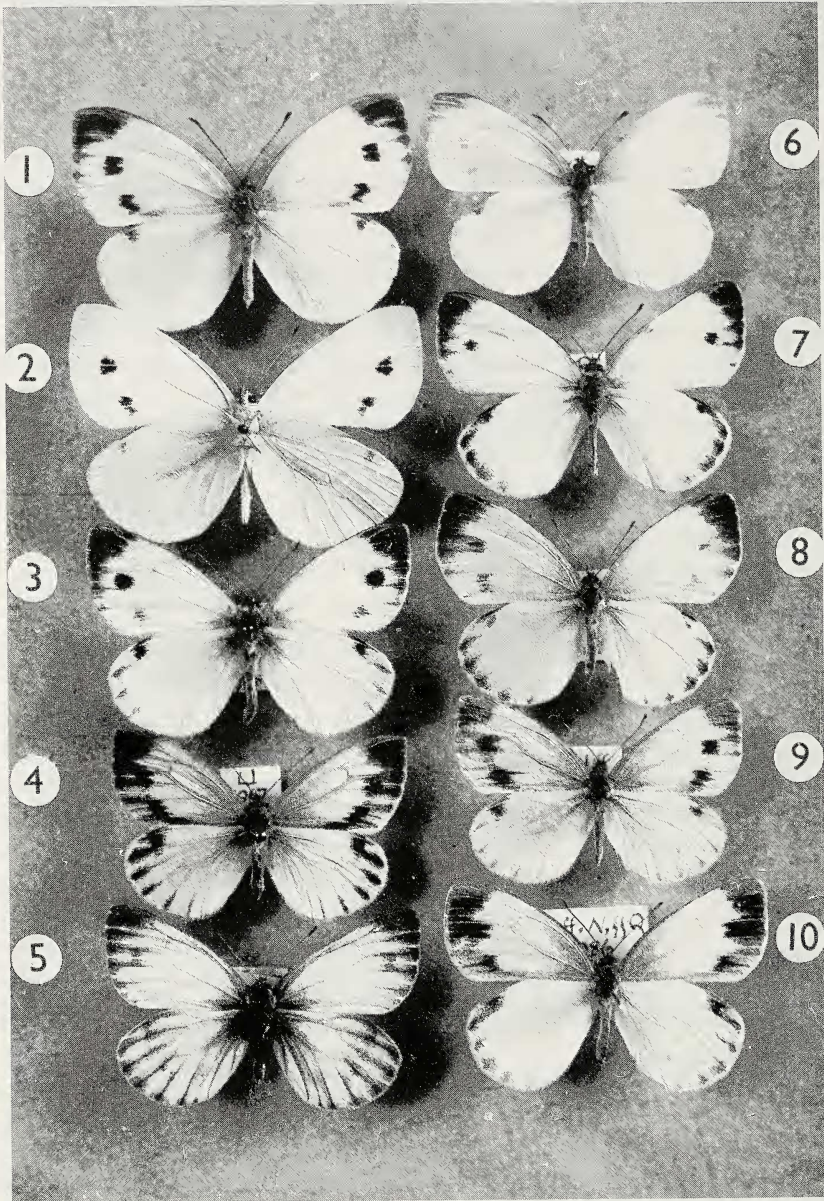
Introduction

A recent paper (Bowden 1988) described the hybridization of *Pieris (napi) macdunnoughii* Remington with European *P. napi* L., and concluded that that the Colorado taxon (like ssp. *marginalis* Scudder of Oregon) carried two genetically distinct systems of yellow coloration. However, no adequate description of the melanic markings of the hybrids was given.

The present publication is intended to supply this, and to discuss the realized expression of the upperside pattern of this species-group, though further experimental work with unrelated *macdunnoughii* material, including European crosses in both directions, is desirable to confirm conclusions, and particularly to quantify environmental effects.

It should be explained that the work now reported was initiated as an attempt to transfer the funebris (Lorković 1971) gene, as homozygote, to substantially pure ssp. *macdunnoughii*. There it might produce an informatively different phenotype. But the series of pairings (starting with an inbreeding of brood 1986-*j* — see below) necessary for this was not obtained, and in the present connection the presence of the funebris gene was probably irrelevant. Any future worker on *macdunnoughii* × *napi* hybridization will avoid this complication, as the funebris gene appears, most unfortunately, to have been lost everywhere.

Several American subspecies related to *Pieris napi* carry no more than faint indications of the spot markings which normally characterize the Palaearctic members of the group (fig. 1). Such indications as there are (e.g. in fig. 6) seem to suggest that the pattern is present, but



1. Corsican ♀'64d^{viii} 6.
2. Corsican ♂'64d^{vi} 59 (underside).
3. Calabrian X Irish ♂'67j 8a.
4. Calabrian X Irish ♀'67j 9a.
5. F₂ *neobryoniae* (ex Kärnten) X *adalwinda* (ex Kiruna) ♂'54p33.
6. *virginiensis* X *oleracea* ♀'65qⁱⁱ 19.
7. Nff.Q ♂'85k1.
8. Q.NffQ ♀'86j2.
9. Q.Nff ♀'86n38.
10. Nff.NffQ ♀'86c15.

has been suppressed. Breeding experiments do reveal the presence in some Nearctic populations of a recessive epistatic gene, *restricta*, which allows apparent dominance of the European marking over its American absence: thus the F₁ hybrids in general follow the European model. This happens, indeed, in the case of *macdunnoughii*.

Summary of Brood Relationships

See also Bowden, 1988.

In the following table, N stands for European *napi* (with or without the funebris gene) and Q stands for *macdunnoughii*. Hybrids are indicated by juxtaposition of these symbols, the female parent being placed first. Lower-case italics identify separate broods.

Q	♀'84R10 × ♂'84R7	→	1985- <i>r</i> ,	14 ♂ + 17 ♀
	♀'85r21 × ♂'85r22	→	1985- <i>q</i> ,	12 ♂ + 11 ♀
NQ	♀'84p27ff × ♂'85r6	→	1985- <i>k</i> ,	95 ♂ + 0 ♀
	♀'86h ^{iv} 10ff × ♂'85q10	→	1986- <i>gⁱ</i> ,	94 ♂ + 0 ♀
	♀'86h ^{iv} 11ff × ♂♂'85q14-16	→	1986- <i>gⁱⁱ</i> ,	10 ♂ + ? 2 ♀
N.NQ	♀♀'85h23,24 × ♂♂'85k67,68	→	1986- <i>c</i> ,	41 ♂ + 36 ♀
Q.NQ	♀'85r31 × ♂♂'85k78,85	→	1986- <i>j</i> ,	5 ♂ + 3 ♀
QN	♀'85q18 × ♂♂'85h88-91	→	1986- <i>n</i> ,	38 ♂ + 26 ♀

Here the symbol ff following an individual identification number indicates a funebris homozygote.

Marking Emphasis in Hybrid Males

In the non-diapause emergence of our F₁ hybrid brood 1985-*k* (fig. 7), which gave no adult females, the black upperside markings of the 39 males were generally intense, with the forewing apical patch extending rather smoothly to vein M1 (= v3 of the Herrich-Schaffer system as used by Higgins & Riley 1970 and Higgins 1975.) So great an extension is usual in *Pieris brassicae* L., but seldom attained in *P. rapae* L. and *P. napi*. Further, the veins of the hindwings were marked distally with spots, which spread laterally from the veins to produce a marginal band only slightly interrupted (fig. 7). However, less extensively marked males were eight in number.

At first sight the almost continuous band recalled the fact that the European mother of 1985-*k* was of funebris form. However, although all the individuals of *k* must have been heterozygous for the (normally recessive) funebris gene, a small proportion (eight as mentioned) showed little or no vein-end expansion. Also, in the similarly constituted later broods 1986-*gⁱ*, *gⁱⁱ*, the hindwing distal vein-marking was less. Such variation, attributable to environmental fluctuation, interferes with quantitative assessment.

Besides, examination of many earlier *napi* f. funebris specimens, especially those of less extreme form, had shown that the marginal band of funebris appears to be built up primarily from interneural

pigmentation, though the veins themselves may also become black. It is known that, in *Pieris* (*Artogeia*), patterns are assembled from systems based on *either* the veins *or* interneural (transverse) bars, and that these systems are separately controlled, whether genetically or by environment. The marking in 1985-*k* is always vein-based, and is in fact close to that of *P. canidia* Sparrman and even of *P. deota* deNiceville. A connection with *funnebris* can probably therefore be excluded.

Markings of Female Hybrids

Females as well as males were obtained when the F_1 males were back-crossed in either direction — as also when, later, the reverse F_1 (♀ *macdunnoughii* \times ♂ *napi* *funnebris* heterozygote) succeeded (1986-*n*).

In the back-cross (1986-*j*) to *macdunnoughii* only about half the offspring should have lacked homozygous *restricta*; accordingly four out of eight expressed European marking. But then as well as the hindwing vein-marking there was heavy black *napi* patterning on the forewings of two females, locally smudged on to small areas usually white (e.g. fig. 8). Such smudging, when it occurred in Lorković's earliest *funnebris* broods, was attributed by him to partial expression of heterozygous *funnebris* (which is normally quite recessive), but I have obtained it (for example) in Calabrian \times Irish *napi* (e.g. fig. 4). It may be that it can occur as some consequence of very wide crosses. Another disturbance in these back-cross females was a certain imbalance: left- and right-side markings were not perfect mirror-images (fig. 8). This feature too may be evidence of an instability (basically genetic) when widely distinct genomes are combined.

In the 1986-*c* back-cross to *napi* (*funnebris* heterozygote) about one-quarter of the offspring (17 or 17 out of 77) were of regular *f. funnebris*, as expected, the phenotypes being within the range generally found (not illustrated here — cf. Bowden 1983). The female $\text{♀}c15$ (fig. 10) looked rather questionable as a possible partial *funnebris*: though its underside showed no *funnebris* characters whatever, this is not conclusive negative evidence. There was little sign of bilateral imbalance in 1986-*c*; most of the non-*funnebris* males looked not unlike the F_1 hybrid males.

In the reciprocal F_1 cross, 1986-*n* (which had relatively few males marked more extensively than *napi* at apices and hindwing vein-ends), the female veins were marked distally, but not very heavily. Some (e.g. $\text{♀}n38$, fig. 9) showed once more a left-right asymmetry of marking. The writer was rather surprised not to find in the females even larger melanic areas, presaged by those unusually extensive male markings in 1985-*k*. But what conclusions are to be drawn from a comparison of figs. 4 and 10?

Pattern Interpretation

There was considerable individual variation within each brood of our hybrids, and a significant diminution of average male patterning between brood 1985-*k* and its successors 1986-*g*^{*i*}, *g*^{*ii*}, though parentage of these was similar (only for 1986-*n* and *c* was the "European" parent merely heterozygous for *funnebris*). As is usual in such cases, it is uncertain exactly how much of this variation was due to cryptic genetic differences, and how much more to environmental fluctuation. But except in 1986-*c*, where *funnebris* became homozygous in some individuals, it is doubtful whether this gene had any visible effect in these *macdunnoughii* hybrids.

Nevertheless, the use of *funnebris*-form *napi* introduced enough possible genetic complications to increase the uncertainty of interpreting the pattern of the hybrids. *Funnebris* itself is far from being understood.

However, we still have much to learn even about the typical *Pieris* (*Artogeia*) design, which is in fact a very peculiar one. Schwanwitsch (1956) claimed that in Pieridae in general the principal wing-pattern components that he recognized as typical for other butterflies were present, but he acknowledged, "Most of the components disappear from the [genus] *Pieris* wing-pattern". There are no eye-spots, no ocelli, no ripple-patterns, no central symmetry system. Even the true discoidal spots (which Nijhout 1978 remarks are "present in virtually every species of Lepidoptera") do not appear, whereas they are prominent in *Euchloe*, *Pontia* and *Tatochila*.

Close hybridization within the sub-genus *Artogeia* usually produces no significant pattern disturbance: the forms that result are simply intermediate, as far as dominant and epistatic relationships allow. More distant hybrids seem to have their specific canalizing mechanisms disoriented, and this can be exaggerated in secondary and back-cross combinations. The pattern of the Arctic/Alpine *adalwinda neobryoniae* F₂ hybrid (fig. 5) is startling in a male, but of course on the underside strong radial markings persist normally in this sex too. It appears that extreme imbalance of modifiers may be responsible for many apparent reversions.

I have previously (1983) quoted Riedl (1978) to support the view that hybridization can allow the re-activation of suppressed gene-systems. It is not intended even to consider here the two questions as to how the basic "*Artogeia*" pattern of these closely related butterflies arose and how its variants are now (for the most part) maintained. The historical question (at present almost beyond conjecture) is of the greater interest. Are ecological/selection proposals convincing?

Pattern and Diapause

Other disturbances are to be expected in wide hybrids, and were in fact encountered in the case of *napi* × *macdunnoughii*. The particularly common failure of the female sex to reach maturity, at least in one direction of the cross (cf. Lorković 1978) has been detailed for these hybrids in our earlier report (Bowden 1988). One amendment to that is due: a second female from 1986-*g*ⁱⁱ eclosed (after diapause) subsequently to the preparation of the report and was classified as a true hybrid, not a waif. So such failure may not be absolute, and I believe that other workers have used injections of ecdysone to induce hybrid females among Papilionidae to complete their imaginal development.

The determination and onset of diapause may also become irregular, or its connection with seasonal forms be distorted.

In brood 1985-*k*, 39 normal non-diapause emergences occurred 25-ix-85 to 1-x-85, then ceased, as if at initiation of diapause, though remaining pupae were not cold-stored until 4-xii-85. However, pupae subsequently restored to room temperature on 12-i-86 and on 27-iv-86 produced 12 + 15 male adults after about 15 days, but still of the non-diapause upperside marking! These "summer-form" insects of February and May 1986 did nevertheless approach the post-diapause underside pattern, with rather complete hindwing veining. On the other hand, pupae kept in the refrigerator until 25-vi-86 and 26-viii-86 produced 12 + 14 "spring-form" males in about eight and five days respectively. These "spring" insects showed only a very slight blackening of upperside hindwing vein-ends.

I believe that the production of "non-diapause" forms after a short but apparently true diapause has perhaps not previously been reported; it deserves study, with stricter environmental control. But all the irregularities of development described above do accord with the author's 1988 conclusion, that *macdunnoughii* Remington is appropriately separated from the species *napi* L.

Acknowledgements. I am very grateful to C. L. Remington, W. B. Watt, Frances Chew and A. M. Shapiro for sending me material of Colorado *macdunnoughii* over a period of 30 years, and also for the background information which they supplied.

Nearly all the specimens obtained in the course of this work are, like others bred by the writer, to be deposited in the British Museum (Natural History), South Kensington, London.

Literature Cited

- BOWDEN, S. R., 1983. A palaeomorph of *Artogeia*? — f. *funnebris* Lorković. Proc. Brit. ent. nat. Hist. Soc. **16**:76-80.
 — 1988. On *Pieris (Artogeia) marginalis macdunnoughii* Remington. J. Res. Lepid. **26**:82-88.
 HIGGINS, L. G., 1975. The Classification of European Butterflies. London.

- HIGGINS, L. G. & N. D. RILEY, 1970. A Field Guide to the Butterflies of Britain and Europe. London.
- LORKOVIC, Z., 1971. *Pieris napi* (L.) morfa funebris, osebujna nova rekombinacija krizanja. Acta entomologica Jugoslavica 7:1-9.
- 1978, Types of hybrid sterility in diurnal Lepidoptera: speciation and taxonomy. Acta entomologica Jugoslavica 14:13-26.
- RIEDL, R., 1978. Order in Living Organisms: a Systems Analysis of Evolution Chichester.
- SCHWANWITSCH, B. N., 1956. Wing-pattern of Pierid butterflies. Revue d'Entomologie de l'URSS 35(2):285-301.